THE FOETAL GROWTH RATES OF WHALES WITH SPECIAL REFERENCE TO THE FIN WHALE, *BALAENOPTERA PHYSALUS* LINN.

BY

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(Plate XIII, text-figures 1–13)

INTRODUCTION

IN the course of an investigation of the reproductive cycle of the southern hemisphere fin whale, *Balaenoptera physalus* Linn., it was necessary to obtain an accurate mean curve of foetal growth in length. It is usual to describe foetal growth in terms of weight, but there are relatively few records of foetal weights of whales owing to the practical difficulties. For present purposes length is therefore much more suitable than weight and as there is a constant relation between length and weight (Text-fig. 13), the curve of growth in length may later be converted to a weight-growth curve by reference to the relatively small number of foetal weight records.

This is an interesting problem quite apart from any indirect use which may be made of the results. The main stimulus for this study was the need to obtain accurate information about the mating season, length of pregnancy and the calving season in the fin whale. It is not possible in this species to study any of these problems directly and in fact the humpback whale, *Megaptera novaeangliae* Borowski, is the only species in which the length of the gestation period and progress of the pairing and calving seasons have been fixed accurately (Chittleborough, 1954, 1958) because this is the only species in which the breeding population has been studied directly in the breeding season. It can therefore be used as a comparative check on the conclusions about other species.

In the fin whale and most other species an indirect approach is necessary because it has not been possible to study the animals in the breeding area.

The most profitable approach to this problem in the fin whale was thought to be a comparison with other species of Mysticetes and with Odontocetes, together with a detailed examination of the data accumulated by 'Discovery' Investigations since 1925 and in recent years by the National Institute of Oceanography. These comprise records of foetal length (snout—notch of flukes) of 956 fin whales and 1112 blue whales (*Balaenoptera musculus* Linn.), together with some records of other species. In addition there are 115 records of foetal weight. These lengths and weights were all measured by biologists or specially trained observers; length records accumulated since 1954 have not been included, but the weight data include records up to the 1957/58 whaling season.

The records of foetal lengths of a number of species given in the International Whaling Statistics from 1932 onwards have not been used. It is well known that these measurements are not accurate, though this in itself will probably not affect an average growth curve. More serious is the fact that small foetuses are almost invariably missed, and as pointed out by Brinkmann (1948), this has the effect of altering the slope of the growth curve.

PREVIOUS WORK

Guldberg (1886), from an examination of the lengths of foetuses of baleen whales in the North Atlantic, was able to show that there is a definite pairing season. Subsequently, more data were collected and reported on by Cocks (a series of papers 1886–90 referred to by Mackintosh and Wheeler, 1929), Grieg (1889), Guldberg (1894), True (1904), Collett (1911), Hamilton (1915), Barrett-Hamilton (Hinton, 1925), and others. An important paper by Risting (1928) was the first attempt at statistical treatment of a large body of data; he gives average growth curves and calculates the standard deviations of the monthly samples.

Hinton (1925) believed that in the southern fin whale, after an initial 61-day period of slow development, growth was probably linear from 30 cm. to birth at 610 cm. and that this regular growth occupied a period of 9 months. By a simple calculation he obtained the dates of pairing from individual foetuses, and made similar calculations for other species. Risting (1928), Zenkovic (1935) and Zemskiy (1950a) also adopted this method. The main points of interest are, first, that initial growth was assumed to be very slow, and secondly, that subsequent growth was assumed to proceed at a uniform rate.

Mackintosh and Wheeler (1929) reviewed the position at that time and came to some important conclusions about the breeding season and foetal growth in blue and fin whales. They first considered the more direct evidence concerning the time of the breeding season. This included information about the seasonal change in the condition of the reproductive organs of both sexes and suggested that the breeding season begins in the earlier part of the southern winter, i.e. in April and May. Examination of foetal length records confirmed this and they concluded that the frequency of pairings is at a maximum in June–July, that gestation lasts for a little less than a year and that 2 years is probably the usual interval between successive pregnancies.

In view of the fact that most later workers on foetal growth of whales have adopted the methods used by Mackintosh and Wheeler (1929), a further brief explanation is called for here. Their own material consisted of eighty-one fin whale and fifty blue whale foetuses, which they plotted graphically according to lengths and the dates on which they were found. The average monthly lengths were also plotted and a 'mean curve of growth' was drawn in by eye 'to represent as well as possible the general trend in the mass of plotted points, regard also being paid to the monthly average lengths' (p. 422). This curve shows a rate of growth which is slow initially and gradually increases throughout pregnancy. The main weakness in this method lies in the uncertainty of the rate of growth in the earliest stages, but this was partly overcome by these authors by fixing the time of the pairing season, as described above, from other sources. They concluded that the gestation periods of blue and fin whales are about $10\frac{1}{4}$ and $11\frac{1}{2}$ months. The former is in fairly close agreement with the conclusions reached in the present paper and the latter estimate is almost identical with them. These methods were applied by Matthews to the humpback whale (1937), the sperm whale, *Physeter catodon* Linn. (1938a) and the sei whale, *Balaenoptera borealis* Lesson (1938b). His conclusions about the length of gestation and the pairing season in the humpback whale are very close to those of Chittleborough (1958) based on more direct evidence. Matthews's figures (figs. 53, 54) in fact show a gestation period of almost 12 months, though he states in the text that gestation takes about 11 months (p. 58). For the sperm whale Matthews shows that growth is linear, which suggests a fundamental difference between this species and the baleen whales. Later authors appear to have overlooked, or ignored, this (Mizue and Jimbo, 1950; Clarke, 1956), and have drawn in a freehand curve.

Paulsen (1939) reviewed Risting's (1928) work and collected information about the occurrence of twinning and multiple foetuses. The next important paper is that by Brinkmann (1948) which

included a section on foetal growth, based on 580 fin whale foetuses and 276 blue whale foetuses whose lengths were recorded by trained Norwegian observers in the Antarctic season 1939/40. This author's conclusions were in very close agreement with those of Mackintosh and Wheeler (1929) concerning the shape of the growth curve for the 4 months, December to March. He showed that for the first 2 months the figures given by the International Whaling Statistics and by Risting (1928) are higher, probably because small foetuses have been overlooked.

Zemskiy (1950b) studied the relation of length to weight in 100 antarctic fin whale embryos and concluded that there were two distinct stages of development characterized by differences in the ratio of length to weight. He also showed that there is no change in body proportions over a range of lengths from 50 to 565 cm. This work will be discussed below.

Jonsgård (1951) discussed the foetal length records available to him for the minke whale (*B. acuto-rostrata* Lacépède) and drew attention to the probable effects of differential migration of pregnant females on the apparent curve of foetal growth.

Post-war observations by Japanese workers are recorded in several papers which deal in aggregate with some thousands of foetal lengths (Mizue and Jimbo, 1950; Nishiwaki and Hayashi, 1950; Nishiwaki and Oye, 1951; Mizue and Murata, 1951; Ohno and Fujino, 1952; Omura, 1953; Sakiura, Ozaki and Fujino, 1953; Kakuwa, Kawakami and Iguchi, 1953; Omura and Sakiura, 1956). The results of this work endorsed previous conclusions, particularly the work of Mackintosh and Wheeler (1929) on blue and fin whales. All these authors were content to draw in curves by eye, without attempting to obtain a mathematical fit to the points. Another important paper on twinning and multiple foetuses in southern fin whales, dealing in part with foetal growth, was contributed by Kimura (1957).

Reference must be made to a short paper by Frazer and Huggett (1958), based on foetal lengths included in the International Whaling Statistics. They conclude that the gestation periods of sperm, humpback, fin and blue whales are respectively 15–16, 12, 9–10 and 9 months. They state that other data suggest that the pilot whale, *Globicephala melaena* Traill, has a gestation period of 16 months.

So far we have been concerned mainly with the baleen whales (*Mysticeti*). The material available for a study of foetal growth in the toothed whales (*Odontoceti*) is much less abundant. The principal papers are those by Guldberg (1894) on four species of odontocetes, by Matthews (1938a), Mizue and Jimbo (1950) and Clarke (1956) on the sperm whale; papers by Degerbol and Nielsen (1930), Vladykov (1944) and Doan and Douglas (1953) on the white whale (*Delphinapterus leucas* Pallas); and an important work by Møhl-Hansen (1954) on the porpoise (*Phocaena phocoena* Linn.). The full results of recent work on the pilot whale (*Globicephala melaena* Traill) are not yet available (Frazer and Huggett, 1958; Sergeant, unpublished; Ann. Rep. Fish. Res. Bd Can., 1954). There are other papers which give less complete information about the course of foetal growth, and estimates of the length of gestation, size at birth, etc., for several species.

Finally, it should be mentioned that Scott (1949) has shown that for ten cetacean species the average neonatal length is directly correlated with adult length (which he defines as an estimate of the maximum length generally attained).

METHODS

Most of the data which are available for different species are sufficient to fix the rates of foetal growth for only part of the gestation period. For the southern fin whale in particular the bulk of the records cover the 6 months October to March, the first two of these months being poorly represented (Text-fig. 9). For some other species the data are perhaps rather more widely spread in time, or cover an earlier part of gestation; for example, the humpback whale, the minke whale, the sperm whale and

the porpoise. These limited curves may be extrapolated forwards to birth and backwards to conception. It is usually possible to estimate the average neonatal length with some accuracy, but the effect of extrapolation on the estimated time of birth can be greatly influenced by uneven sampling caused by differential migration of pregnant females (see below). The difficulty about finding the average date of conception by this method is that the rate of growth in the first 2 months is very slow. One approach is to take a species such as the humpback whale for which the average dates of conception and calving have been established, as well as the growth of the foetus over part of gestation. Then by analogy the growth rate in the early months can be estimated for other species. Freehand extrapolation and analogy do not provide a very firm basis, and the detailed conclusions drawn from growth curves constructed in this way may be greatly in error.

A better approach is to see whether it is possible to make any mathematical generalizations about foetal growth by combining the data which are available from all sources, for a variety of species, concerning foetal lengths, and mating and calving seasons.
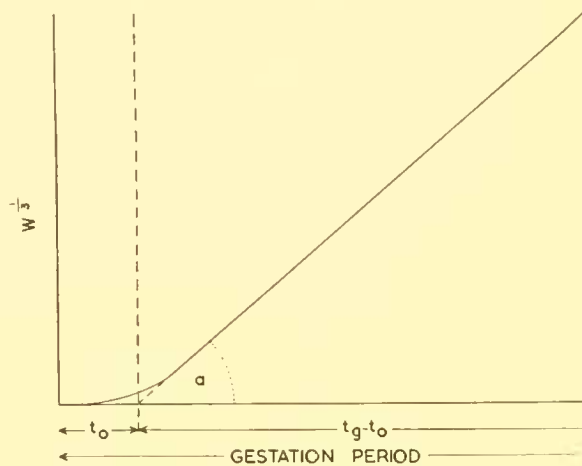
Text-fig. 1. Diagram illustrating relation between foetal weight (or length), gestation period, t_0 and a (after Huggett and Widdas, 1951).

In this respect the work of Huggett and Widdas (1951) provides a starting point. These authors showed that for a variety of mammals of widely different mammalian orders the cube root of the foetal weight gave a linear plot with age for all except the first part of pregnancy. They suggested that the beginning of this steady state of growth might be correlated with the full establishment of the placental circulation. Previously to this work they had shown that foetal length increases linearly with age.

Their hypothesis is expressed in the general formula $W^{\frac{1}{3}} = a(t - t_0)$ and since $W \propto L^3$ it follows that $L = a(t - t_0)$. The term a is constant in respect of any particular species and is called by them the 'specific foetal growth velocity'. It is the slope of the line relating foetal weight, $W^{\frac{1}{3}}$ (or foetal length, L) to the age after conception (t) in that segment of the growth curve where the relationship is linear. The term t_0 'is the intercept where the linear part of the plot, if produced backwards, cuts the time axis' (see Text-fig. 1). This term has 'no clear biological significance in foetal development, but if the numerical value of t_0 can be estimated by analogy with other mammals...then one known weight (W) and time from conception (t) would be sufficient to determine the value of a for the mammal concerned'. Their estimate of t_0 for different animals is based on the observation that t_0 increases as the gestation time lengthens but forms a decreasing fraction of the total gestation time. Huggett and Widdas use arbitrary estimates of t_0: for gestation times from 0 to 50 days $t_0 \fallingdotseq 0 \cdot 4 \times$ (gestation time); 50–100 days, $t_0 \fallingdotseq 0 \cdot 3 \times$ (gestation time); 100–400 days $t_0 \fallingdotseq 0 \cdot 2 \times$ (gestation time); and over 400 days $t_0 \fallingdotseq 0 \cdot 1 \times$ (gestation time). These estimates of t_0 apply to weight data and for length t_0 is slightly less.

For example, in the sheep $Wt_0 = 38.6$ days and $Lt_0 = 34$ days. In the present paper Lt_0 is assumed to be $0.9 \times Wt_0$, and Huggett and Widdas's scale of estimates of Wt_0 is converted by this factor.

Huggett and Widdas state that the growth velocity found by their method for blue and fin whales is 'at least $2\frac{1}{2}$ times greater than the highest rate found for all other mammals, and about 10 times greater than the rate for Primates'. They remark that it 'would be interesting to see if these high rates are peculiar to the large whales or are the same in related species of smaller size'. It is generally considered that the Odontocetes are on average on a lower grade than Mysticetes (Simpson, 1945) and in general they are smaller, so they will now be discussed in this order. Conspicuous modifications in the shape as well as the magnitude of the foetal growth curves of the Mysticetes as compared with the Odontocetes then become apparent.

TOOTHED WHALES (ODONTOCETI)

Data on the foetal growth of the sperm whale given by Matthews (1938a), Mizue and Jimbo (1950), and Clarke (1956) have been used. As the full original data are not given the mean monthly foetal lengths have been taken from the graphs and the Japanese measurements have been converted from
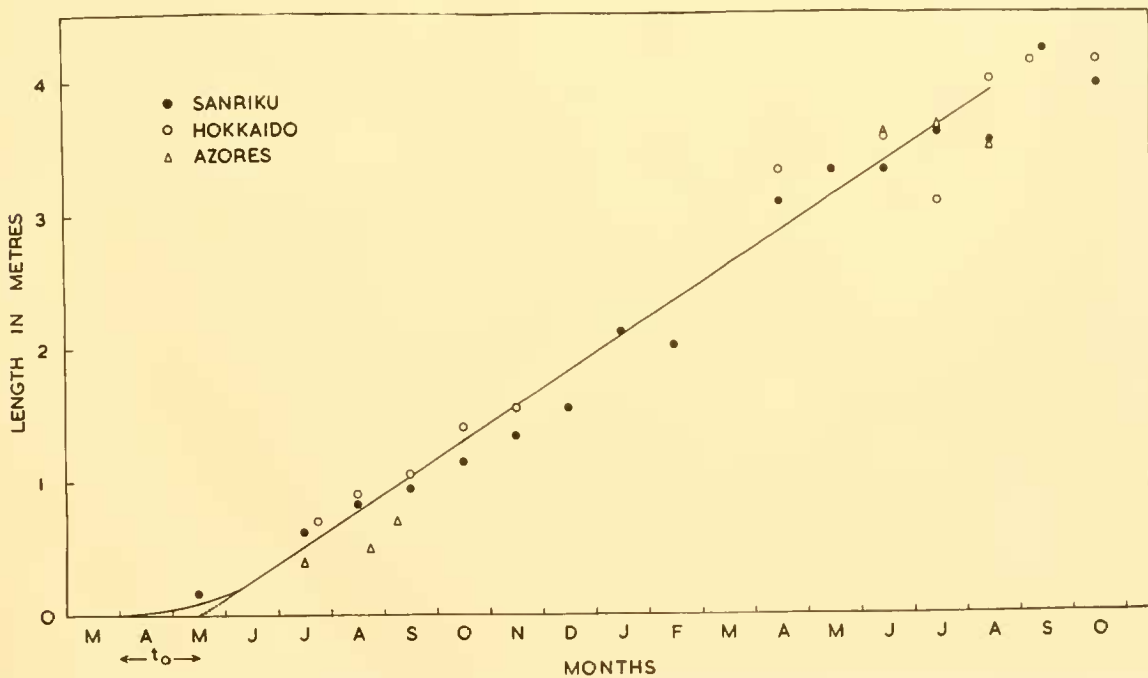
Text-fig. 2. Foetal growth in length of northern hemisphere sperm whale, *Physeter catodon* (points represent monthly means). In drawing the average growth curve only the North Pacific data have been used.

feet to metres in the interests of uniformity. Although great care was exercised, some small errors may have resulted from this treatment, but it is thought that they do not affect the conclusions drawn.

These data are set out graphically for northern and southern hemisphere sperm whales in Text-figs. 2 and 3. The average neonatal lengths are taken to be 3.92 m. in the northern hemisphere (Clarke, 1956) and 4.15 m. in the southern hemisphere (Matthews, 1938a, p. 138, '4 metres or a little more'). Lines representing the average rate of growth have been fitted by inspection, slightly weighted to allow for the variation in size of the monthly samples. Both northern and southern hemisphere data suggest that growth is linear for most of gestation. For the northern data the length of the period $(t_g - t_0)$ is 15 months, or 457 days. If the neonatal length of southern hemisphere sperm whales is

assumed to be 4·15 m. then this part of gestation is again 15 months. For foetal weight data Huggett and Widdas's (1951) arbitrary scale suggests that Wt_0 is about $0·08 \times$ (gestation time) for gestation periods of 450–500 days and converting, $Lt_0 \simeq 0·07 \times$ (gestation time). Then $Lt_0 \simeq (0·07 \times 457)/0·93 \simeq$ 34 days and the total gestation period is 491 days or 16 months. This agrees well with previous estimates (16–17 months) which have taken account of other evidence of the pairing and calving season, and also the bimodal frequency distribution of foetal lengths.

The steeper growth curve of the foetal sperm whale in the southern hemisphere, and also the larger neonatal size of the southern animals, is in line with work on other cetaceans showing that southern hemisphere adults are larger than those in the north (e.g. Jonsgård, 1952; Pike, 1953). Clarke (1956, p. 289) has already suggested that both male and female sperm whales attain larger sizes in the southern hemisphere.
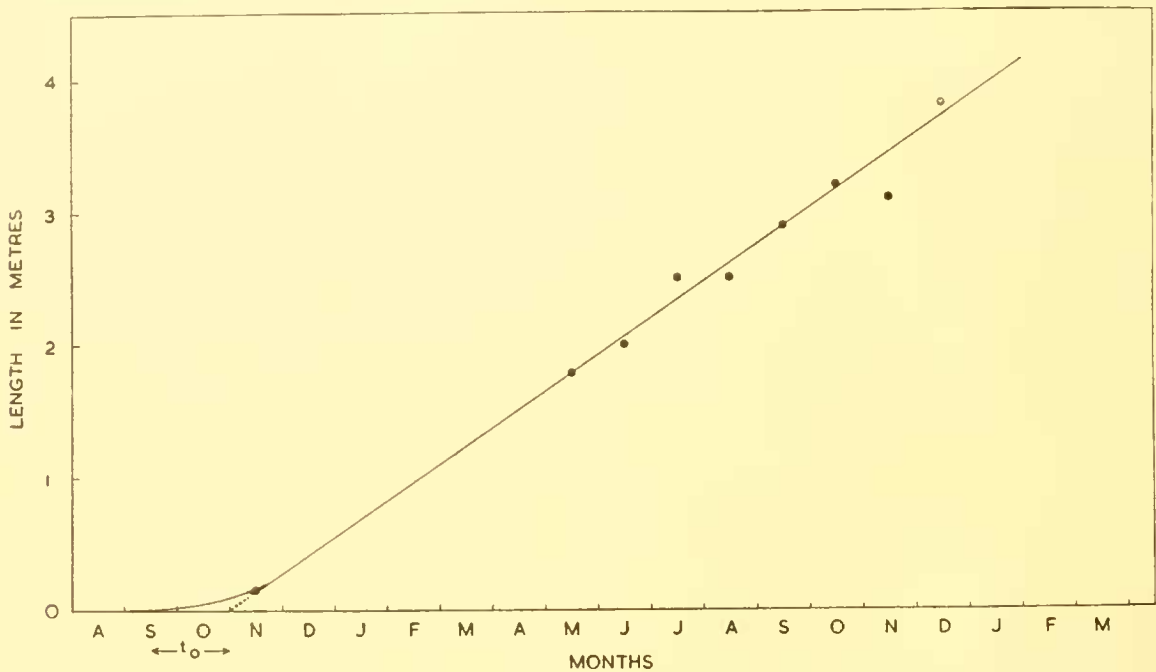
Text-fig. 3. Foetal growth in length of southern hemisphere sperm whale, *Physeter catodon* (points represent monthly means).

For the porpoise, Møhl-Hansen (1954) gives data on the length of 119 foetuses from the Baltic. Of the females judged to be sexually mature 84% were pregnant; there were not two foetal length groups, and this together with other data gives striking evidence that the gestation period is under a year. He estimates that pairing occurs in July and August and that the duration of pregnancy 'should be 11, or at least 10–11, months, instead of 9–10 as usually assumed' (p. 389). The average neonatal length is approximately 75 cm. These data are presented graphically in Text-fig. 4, in which Mohl-Hansen's mean monthly values for November to February are shown; also three individual length records from the Zoological Museum, Copenhagen, and three individual records from Holland (Van Deinse, 1946). The Norwegian material for the porpoise (Grieg, 1898; Møhl-Hansen, 1954, fig. 7) shows a higher growth rate than the material from Denmark and Holland; it is not used here. The line fitted by inspection attains 75 cm. at the end of June and intersects the abscissa in the second half of September giving an estimate of $9\frac{1}{4}$ months (or 282 days) for $(t_g - t_0)$. For gestation periods of a little over 300 days, using Huggett and Widdas's estimate converted for length, $Lt_0 \simeq 0·15 \times$ (gestation time) and therefore $Lt_0 \simeq (0·15 \times 282)/0·85 \simeq 50$ days.

The total gestation period estimated in this way is therefore 332 days or nearly 11 months, which is in close agreement with Møhl-Hansen's (1954) estimate. The peak time of conceptions is the beginning

of August, which also agrees very well with this author's conclusions; peak calving is estimated as the end of June and does not seriously conflict with the information given by him.

Limited data are published by Vladykov (1944) and Doan and Douglas (1953) from studies of the white whale in the Saint Lawrence area and Hudson Bay, respectively. These are set out in Text-fig. 5 from which it appears that in this species also foetal growth can be described by a linear plot, with parturition at the end of June and Lt_0 in the middle of June, so that the estimate of (t_g-t_0) is $12\frac{1}{2}$ months, or 380 days. For gestation periods of this magnitude Lt_0 is estimated to be $0\cdot 1 \times$ (gestation time). Then $Lt_0 \simeq (0\cdot 1 \times 380)/0\cdot 9 \simeq 42$ days. The gestation period is therefore estimated to be 422 days,
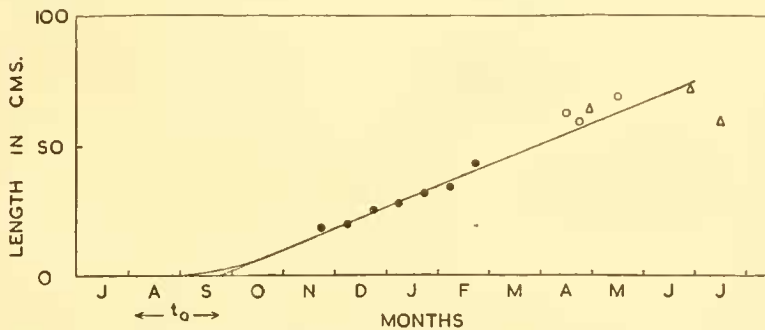
Text-fig. 4. Foetal growth in length of the porpoise, *Phocaena phocoena*. Black circles, monthly means, Denmark; white circles, single records, Denmark; white triangles, single records, Holland.
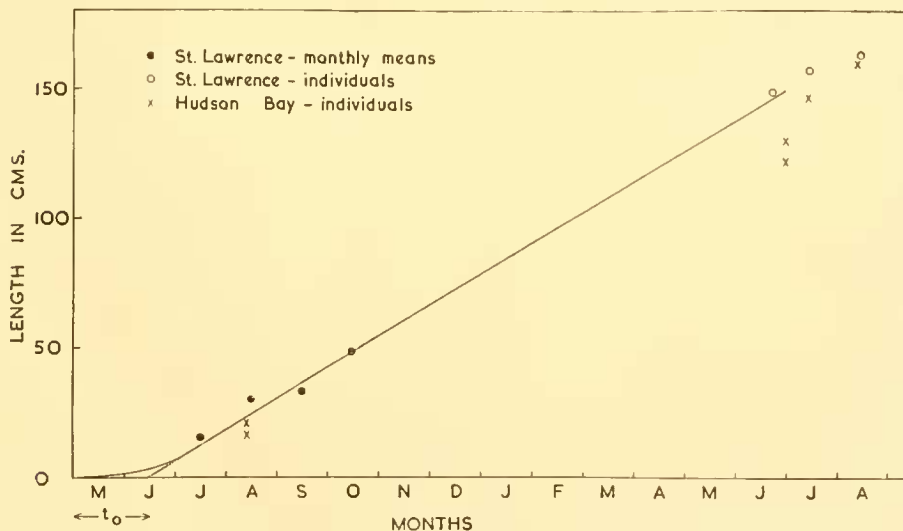
Text-fig. 5. Foetal growth in length of the white whale, *Delphinapterus leucas*.

or just under 14 months, with the majority of conceptions in April and May and birth at an average length of 1·5 m. taking place about the end of June. This is not in close agreement with the tentative conclusions of Vladykov (1944) and Doan and Douglas (1953).

In the Greenland area this species has been studied by Degerbol and Nielsen (1930) who give lengths of 131 foetuses measured in the 6 months, November to April. Their data also suggest that after the initial period growth is linear, but the slope of their growth curve is steeper, and the neonatal length evidently greater, than in the Canadian populations. It is not possible to estimate the gestation period from these data.

For these three species of toothed whales the foetal growth in length can be described by a linear plot over most of the period of gestation and the estimates of the length of the gestation period by means of Huggett and Widdas's (1951) method are in fairly close agreement with previously published

estimates. The assumption (from rather sparse data) that Lt_0 is 90% of Wt_0 appears to be justified and the length of the estimated period Lt_0 varies from 34 days in *Physeter* to 50 days in *Phocaena*.

Huggett and Widdas (1951, p. 413) remark that 'among mammals in the intermediate range of [their] Fig. 8, the period of linear growth is determined by the size of the foetus at birth. Thus, as the birth weight of the young is increased the mammal does not grow its young quicker, along a steeper slope, but must grow its foetus for a longer time.' This is now seen not to be entirely true of the toothed whales in which the slope of linear growth may be steeper and also continued for a longer time, as for instance in the sperm whale compared with the porpoise. This answers the question put by Huggett and Widdas (1951) (see p. 287), and shows that Rubner's finding (1908) that, in all species except man, the birth weight is proportional to the gestation time, is not true of the toothed whales. As will be apparent when the position in baleen whales has been established, it is even less applicable to whales in general.

BALEEN WHALES (*MYSTICETI*)

The only group of whalebone whales in which foetal growth has been studied in any detail are the Balaenopterids. The principal papers are listed in an earlier section of this paper.

In all species of Balaenopterids and in the grey whale, *Eschrichtius gibbosus* Erxleben (Hubbs, 1958), the gestation period has been fixed at a year or less. Records of mean monthly foetal lengths, evidence of the pairing season from examination of male and female reproductive tracts, of the occurrence of calves, and of the proportion of mature females which are pregnant, all point to this conclusion. Indeed, it is evident that in some species females commonly undergo two pregnancies in 2 years (Jonsgård, 1951; Omura and Sakiura, 1956) and in others it is not uncommon (Chittleborough, 1958; Laws, 1958; Hubbs, 1958).

The neonatal lengths are known fairly accurately for most species and adequate foetal length records cover several months of the gestation period in these species (Text-fig. 12). When the mean monthly foetal lengths and the neonatal lengths are plotted, it is immediately apparent that if the gestation period for these species is a year or less, foetal growth in length cannot be described by a straight line as in the Odontocetes discussed above. Instead it appears that the slope of the growth curve, 'gradually increases throughout pregnancy' as Mackintosh and Wheeler (1929) showed for blue and fin whales. It should be pointed out that even in these two species, which are the fastest growing whales, more than two straight lines are necessary in order to fit the points and at the same time to give a gestation period of a year or less.

A number of trial plots were made at first and these suggested that the first half of foetal growth was linear (as in the toothed whales), while the data for the second part agreed quite well with an exponential growth rate.

The humpback whale is the species in which the duration of pregnancy has been fixed with most precision (Chittleborough, 1954, 1958). In Text-fig. 6 a curve of foetal growth in length has been constructed for this species. The method has been to take the mean dates of conception and calving as early August, so that the gestation period is 12 months, and the neonatal length given by Chittleborough (1954, 1958) has been plotted accordingly. The mean monthly foetal lengths given by Matthews (1937) have been used and also the mean foetal length for a sample taken in the first week in February, given by Symons and Weston (1958). The monthly means from March onwards are based on very small samples and have not been plotted. A linear plot has been fitted to the foetal length values for September to January and has been continued as an exponential curve up to the neonatal point. The linear part of the curve intersects the abscissa at the end of the first week in September, giving a value for Lt_0 of approximately 38 days. The slope of the linear segment of the

curve is slightly less than the slope of the sperm whale curve (Text-fig. 12) and Lt_0 is very close to this value for the sperm whale in which $Lt_0 \simeq 34$ days.

This suggests that it is correct to interpret the middle phase of foetal growth as linear in the humpback whale at least and probably this also holds good for other baleen whales. The exponential fit to the second part does not rest on a firm foundation and, as will be seen in the more detailed
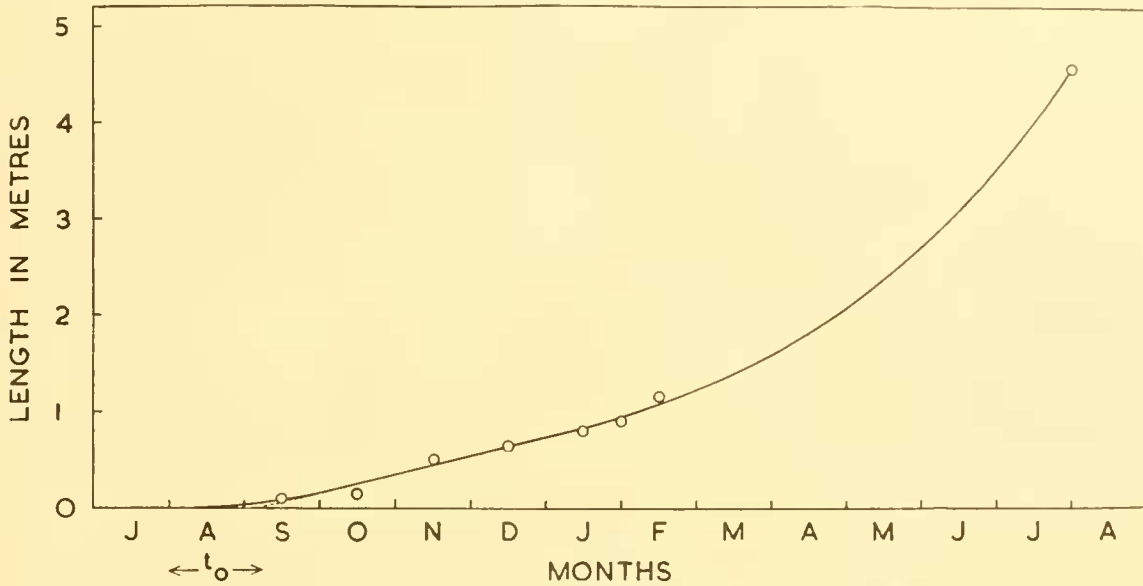
Text-fig. 6. Foetal growth in length of southern hemisphere humpback whale, *Megaptera novaeangliae*.
Points are mean values. See text for explanation.
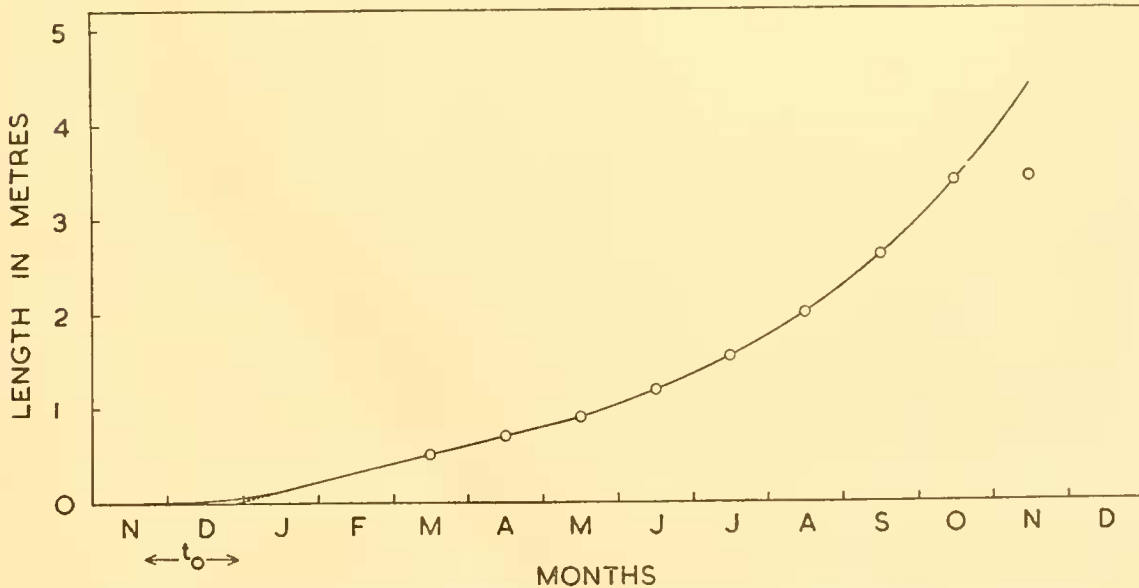
Text-fig. 7. Foetal growth in length of northern hemisphere sei whale, *Balaenoptera borealis*.
Points represent monthly means.

discussion of blue and fin whales, the variability in the monthly foetal lengths is such that foetal growth could be described by a series of linear phases of different slope, or by a more complicated general formula. The logarithmic plot has been accepted as the most simple fit for all the species considered.

As foetal growth of baleen whales cannot be described by a linear plot of foetal length throughout gestation, the values of Lt_0 cannot be derived by reference to the length of gestation. However, it is

found that for the four species considered so far (in which Lt_0 has been estimated from the length of gestation (toothed whales), or by reference to an accurately fixed conception date (humpback whale)), the slope of linear growth is closely correlated with Lt_0 (Table 1). As the correlation is so close the values of Lt_0 for other species in which a is known have been obtained by extrapolation (blue and fin whale) or interpolation (northern sei whale, minke whale). These values are bracketed in Table 1.

For the northern sei whale (*Balaenoptera borealis* Lesson), the mean monthly foetal length values given by Mizue and Jimbo (1950) fit almost exactly a linear/log growth curve. The three points for March, April and May fall on a straight line intersecting the abscissa at the end of December, and the five means for the succeeding months, June to October, fall on a logarithmic curve (Text-fig. 7). Moreover, the neonatal length given by Mizue and Jimbo (1950) for this species (14–15 ft., or about 4·4 m.) is very close to the length of the humpback whale at birth and the fitted curves of these two species are almost identical (Text-fig. 12). If Lt_0 can be taken to be 39 days (Table 1) then the average date of conception is in the third week in November. By extrapolation of the exponential growth

Table 1. *Values of* Lt_0 *and* a *for eight cetacean species*

Species	Lt_0	a
Physeter catodon	34	0·84
Delphinapterus leucas	42	0·47
Phocaena phocoena	50	0·25
Megaptera novaeangliae	38	0·70
Balaenoptera musculus	(30)	1·00
B. physalus	(33)	0·88
B. borealis	(39)	0·66
B. acutorostrata	(43)	0·49

curve in the second half of pregnancy the birth length is reached in mid-November, so the gestation period estimated in this way is almost 12 months. Mizue and Jimbo (1950) also assume that the end of November is the average time of birth, but that the time of pairing is in January, giving a gestation period of less than 11 months. It should, however, be noted that these authors fix the time of conception by freehand extrapolation.

Since the work of Mizue and Jimbo (1950), Omura and Fujino (1954) have shown that the northern and southern types of sei whale in the western Pacific Ocean are the species *B. borealis* Lesson, and *B. brydei* Olsen, respectively. These two species are similar in size, the former being apparently slightly larger. The main differences are in the quality and shape of the baleen plates, the shape of the palate, and the extent of the ventral grooves. The catch at the Bonin Islands is now composed of Bryde's whales, but formerly, when the material in Mizue and Jimbo's (1950) paper was collected, the whaling season was earlier and the catch was almost entirely composed of sei whales. According to Omura and Fujino (1954) sei whales are taken at the Bonin Islands from November to April and in May and June the catch is composed of Bryde's whales; at Sanriku and Hokkaido the catch is almost entirely sei whales.

It seems reasonable, therefore, to conclude that the data presented in Text-figure 7 apply to the sei whale, *B. borealis*. In view of the similarity in the size of *B. borealis* and *B. brydei* it is probable that the average neonatal lengths and foetal growth curves are similar, though the breeding season may be different.

The mean monthly foetal lengths for July to October of the northern fin whale given by Mizue and Jimbo (1950) also lie on an exponential curve.

The foetal growth of the minke whale has been discussed by Jonsgård (1951) and Omura and Sakiura (1956). There is no reliable information on the length of gestation but Jonsgård found that only

4·5% of the adult females examined were non-pregnant, and all lactating females were pregnant. This strongly suggests that the gestation period is less than 12 months (as there are not two foetal length groups) and Jonsgård concluded that 'the majority of mature females bring forth young once a year'. His material covers too short a period to allow for an estimate of the duration of gestation. Nor is an estimate of the length of gestation possible from the data available to Omura and Sakiura (1956). Earlier estimates of the duration of gestation as 10 months, made by Eschricht and Guldberg are referred to by Jonsgård (1951), who concludes that pairing occurs from about January to the end of May, with a maximum frequency probably in March. For reasons which Jonsgård discusses, Grieg's (1889) material has not been used in the present paper. Although Jonsgård has concluded that, owing to differential migration, the foetal measurements available are not truly representative of the stock of whales, his mean lengths for the 4 months April to July are very similar to those given by Omura and Sakiura (1956, fig. 23, curve A).

The growth curve for these months appears to be linear as in other species (Text-fig. 12) and intersects the abscissa at Lt_0 in mid-March. By analogy with other species the period from conception to Lt_0 is probably about 43 days (i.e. intermediate between the humpback whale and the porpoise) which gives an estimated average date of conception at the beginning of February. It is not possible to come to any conclusions about the later part of pregnancy, but with a neonatal length of 2·46 m. (Jonsgård, 1951) or even 2·8 m. (Omura and Sakiura, 1956) the rate of growth must increase markedly if pregnancy is to occupy no more than 12 months.

The evidence presented so far strongly suggests that, in a baleen whale species foetal growth in length may be represented by a curve, increasing very slowly at first, then linearly for about 4 months, and finally increasing exponentially until parturition. Although the strong measure of agreement between the different species, and particularly between the estimated and observed conception dates for the humpback whale, is very suggestive, it must not be forgotten that mean values of small samples may differ considerably from the true mean value in the population sampled, and the evidence for a phase of exponential growth is not conclusive.

FIN AND BLUE WHALES

The foregoing parts of this paper have been concerned with published data, and without the full original records it was not possible to calculate the extent of variation within the monthly samples.

For 956 southern hemisphere fin whales and 1112 blue whales the original data on foetal lengths are available and will now be used in a more detailed study of foetal growth in these species in order to test the hypothesis put forward above.

Of the fin whale records, five are from Saldanha Bay, South Africa, 268 are from South Georgia and 683 are from the pelagic whaling grounds. The South Georgia sample extends by 2 months the period of foetal growth covered by the pelagic data. Of the blue whale records, seven are from Saldanha Bay, and ninety are from South Georgia. As they do not extend the period for which data are available they are not used in calculating the monthly means.

All these measurements were made either by biologists or by specially trained observers, and the sources of error may therefore be considered to be minimal[1]. The foetal length records are summarized in Tables 2 and 3; conclusions about the growth curves are presented in Tables 4 and 5 and Text-fig. 8.

The variability of the length records is indicated by the mean plus or minus two standard errors. There is a 95% probability that the true mean of the population as a whole, in any one month, assuming the sample is not biased, will lie within this range. For the fin whale the value of four

[1] For example, the uterus is searched for a small foetus if a functional corpus luteum is seen in the ovaries.

Table 2. *Records of foetal lengths of southern hemisphere fin whales (Antarctic pelagic and South Georgia). Length groups are given to the first decimal place and, for example, group 1·0–1·2 is to be taken as 1·01–1·20.*

Length (m.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
0·0–0·2	1	3	3	2	—	—	—	9
0·2–0·4	3	5	9	14	2	—	—	33
0·4–0·6	2	1	10	10	4	—	—	27
0·6–0·8	5	9	13	18	7	4	—	56
0·8–1·0	4	5	21	20	6	4	—	60
1·0–1·2	3	14	8	14	8	3	—	50
1·2–1·4	3	5	15	24	19	6	—	72
1·4–1·6	1	10	2	22	13	6	—	54
1·6–1·8	—	4	14	20	14	9	—	61
1·8–2·0	—	1	15	23	15	5	—	59
2·0–2·2	—	1	10	19	10	6	1	47
2·2–2·4	—	1	10	14	20	7	—	52
2·4–2·6	—	—	4	18	19	10	—	51
2·6–2·8	—	—	6	9	26	5	1	47
2·8–3·0	—	—	2	16	20	13	—	51
3·0–3·2	—	—	—	11	16	10	1	38
3·2–3·4	—	—	—	4	7	5	—	16
3·4–3·6	—	—	—	1	13	14	—	28
3·6–3·8	—	—	—	4	18	10	—	32
3·8–4·0	—	—	—	3	14	10	—	27
4·0–4·2	—	—	—	1	14	8	—	23
4·2–4·4	1	—	—	3	5	10	—	19
4·4–4·6	—	—	—	—	8	3	1	12
4·6–4·8	—	—	—	—	4	5	1	10
4·8–5·0	—	—	—	—	1	4	—	5
5·0–5·2	—	—	—	—	—	3	—	3
5·2–5·4	—	—	—	—	1	2	—	3
5·4–5·6	—	—	—	—	—	1	—	1
5·6–5·8	—	—	—	—	—	—	1	1
5·8–6·0	—	—	—	—	—	2	—	2
6·0–6·2	—	—	—	—	—	—	1	1
6·2–6·4	—	—	—	1	—	—	—	1
Total	23	59	142	271	284	165	7	951

Table 3. *Records of foetal lengths of southern hemisphere blue whales (Antarctic pelagic only). Length groups as in Table 2*

Length (m.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
0·0–0·2	—	—	1	—	—	—	—	1
0·2–0·4	—	3	2	1	—	—	—	6
0·4–0·6	—	3	7	3	—	—	—	13
0·6–0·8	—	2	5	4	1	—	—	12
0·8–1·0	—	1	17	12	4	—	—	34
1·0–1·2	1	2	7	6	—	—	—	16
1·2–1·4	—	8	30	24	8	2	—	72
1·4–1·6	—	3	32	28	6	2	—	71
1·6–1·8	1	4	11	5	1	—	—	22
1·8–2·0	—	4	32	34	9	1	—	80
2·0–2·2	—	2	17	22	13	1	—	55
2·2–2·4	—	—	7	15	2	—	—	24
2·4–2·6	—	1	25	37	16	5	—	84
2·6–2·8	—	—	15	33	20	3	—	71
2·8–3·0	—	—	1	1	2	1	—	5
3·0–3·2	—	—	13	40	13	6	—	72
3·2–3·4	—	—	7	30	13	7	—	57
3·4–3·6	—	—	1	4	1	1	—	7
3·6–3·8	—	—	4	29	27	4	—	64
3·8–4·0	—	—	1	14	22	9	1	47
4·0–4·2	—	—	—	1	5	1	—	7
4·2–4·4	—	—	1	19	16	7	1	44
4·4–4·6	—	—	1	11	19	11	—	42
4·6–4·8	—	—	—	1	3	2	—	6
4·8–5·0	—	—	—	8	10	8	—	26
5·0–5·2	—	—	—	3	11	9	—	23
5·2–5·4	—	—	—	—	—	—	—	—
5·4–5·6	—	—	—	1	15	9	—	25
5·6–5·8	—	—	—	1	4	2	—	7
5·8–6·0	—	—	—	—	1	—	—	1
6·0–6·2	—	—	—	—	1	5	—	6
6·2–6·4	—	—	—	—	1	3	—	4
6·4–6·6	—	—	—	—	—	—	—	—
6·6–6·8	—	—	—	—	1	2	—	3
6·8–7·0	—	—	—	—	1	—	—	1
7·0–7·2	—	—	—	—	1	—	—	1
7·2–7·4	—	—	—	—	1	—	—	1
Total	2	33	237	387	248	101	2	1010

Table 4. *Growth in length of southern hemisphere fin whale embryos. See text for explanation*

| Month	Size of sample	Mean length (m.)	2 S.E.	Fitted curve
Early June	—	—	—	0·00
Mid-July	—	—	—	0·10
Mid-August	3	—	—	0·30
Mid-September	2	—	—	0·55
Mid-October	23	0·809	0·158	0·80
Mid-November	59	1·069	0·128	1·07
Mid-December	142	1·377	0·121	1·33
Mid-January	271	1·775	0·112	1·82
Mid-February	284	2·620	0·128	2·55
Mid-March	165	3·056	0·188	3·40
Mid-April	7	4·128	1·154	4·70
Mid-May	—	—	—	6·40
Total	956	—	—	—

Table 5. *Growth in length of southern hemisphere blue whale embryos. See text for explanation*

Month	Size of sample	Mean length (m.)	2 S.E.	Fitted curve
Mid-May	—	—	—	0·00
Mid-June	—	—	—	0·06
Mid-July	2	—	—	0·18
Mid-August	2	—	—	0·45
Mid-September	2	—	—	0·75
Mid-October	6	1·153	—	1·05
Mid-November	33	1·300	0·199	1·35
Mid-December	237	1·896	0·104	1·90
Mid-January	387	2·682	0·109	2·63
Mid-February	248	3·597	0·168	3·60
Mid-March	101	4·258	0·246	5·10
Mid-April	2	—	—	7·00
Total	1022	—	—	—

standard errors is about 0·26 m. Even in January and February, in which the sample sizes are large, the variation is of this order. The explanation of this relatively large variation is undoubtedly that the pairing season extends over several months, thus increasing the length variation within the monthly samples. Comparison of Tables 4 and 5 shows that a similar variation occurs in the blue whale.

Symons (1955) compared foetal length data for fin whales taken in area IV in 1954 and in areas III and IV in 1955[1], and suggested that those in the second year were 'some 1 to 2 weeks late in their peak period of conception'. He then put forward a hypothesis based on this supposed difference.
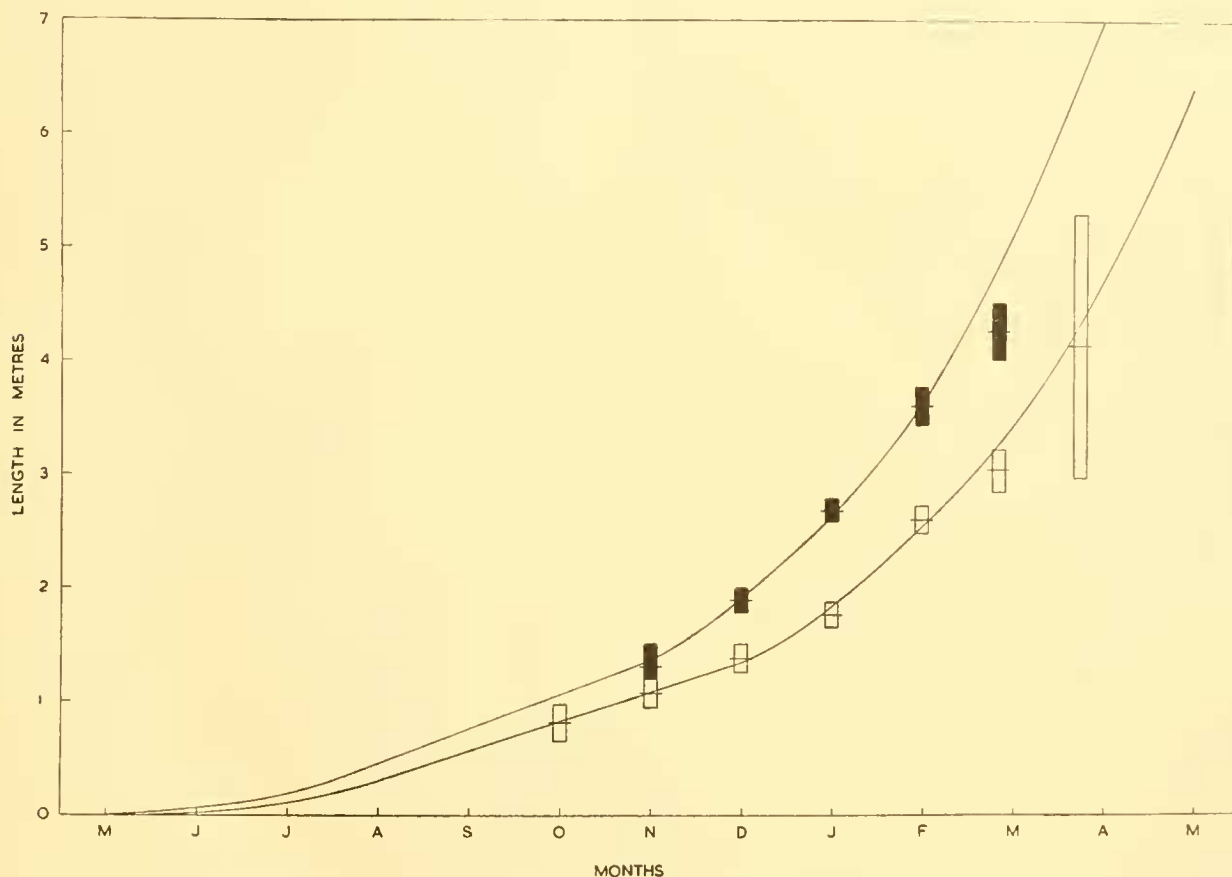
Text-fig. 8. Foetal growth in length of southern hemisphere blue whale, *Balaenoptera musculus*, and fin whale, *B. physalus*. Rectangles represent monthly means, plus or minus two standard errors. (Black—blue whale; white—fin whale).

In fact the greatest differences between his mean lengths are almost within the range of four standard errors (about 0·26 m. or 10 in.) calculated for the present material and certainly well within plus or minus two standard errors of the means for his very much smaller samples. The supposed difference between these two years is therefore unlikely to be significant.

The average growth curve for the fin whale has been fitted as follows. The mean foetal lengths of the samples for October, November and December are thought to be very close to the true mean lengths for these months; they lie on a straight line which cuts the abscissa, when extrapolated, in mid-July. The slope of this line is very similar to that calculated for the sperm whale (Text-fig. 12) and the period from conception to Lt_0 is estimated to be 33 days in the fin whale (Table 1). This gives the second week in June as a mean conception date for the southern hemisphere fin whale, which agrees very well with independent conclusions from other data. (These include the follicular cycle of females at puberty, and the histological cycle of testis activity and of testis tubule diameters,

[1] There are six Antarctic whaling 'areas'. Areas III and IV are south of the Indian Ocean.

which will be described in a later paper.) It should be noted that this conclusion is in agreement with that reached by Mackintosh and Wheeler (1929) on similar grounds.

A second straight line of different slope can be drawn through the blocks marking the means plus or minus two standard errors shown for January, February, March and April in Text-fig. 8. When extrapolated this gives an impossibly long gestation period. In any case the true monthly means of the population are probably well within the range of four standard errors, and in addition it can be shown that the samples for March and April are biased towards lower values, owing to differential migration of females from the area (discussed below). A logarithmic curve has therefore been fitted to the mean lengths for December, January and February. When extrapolated this attains the mean
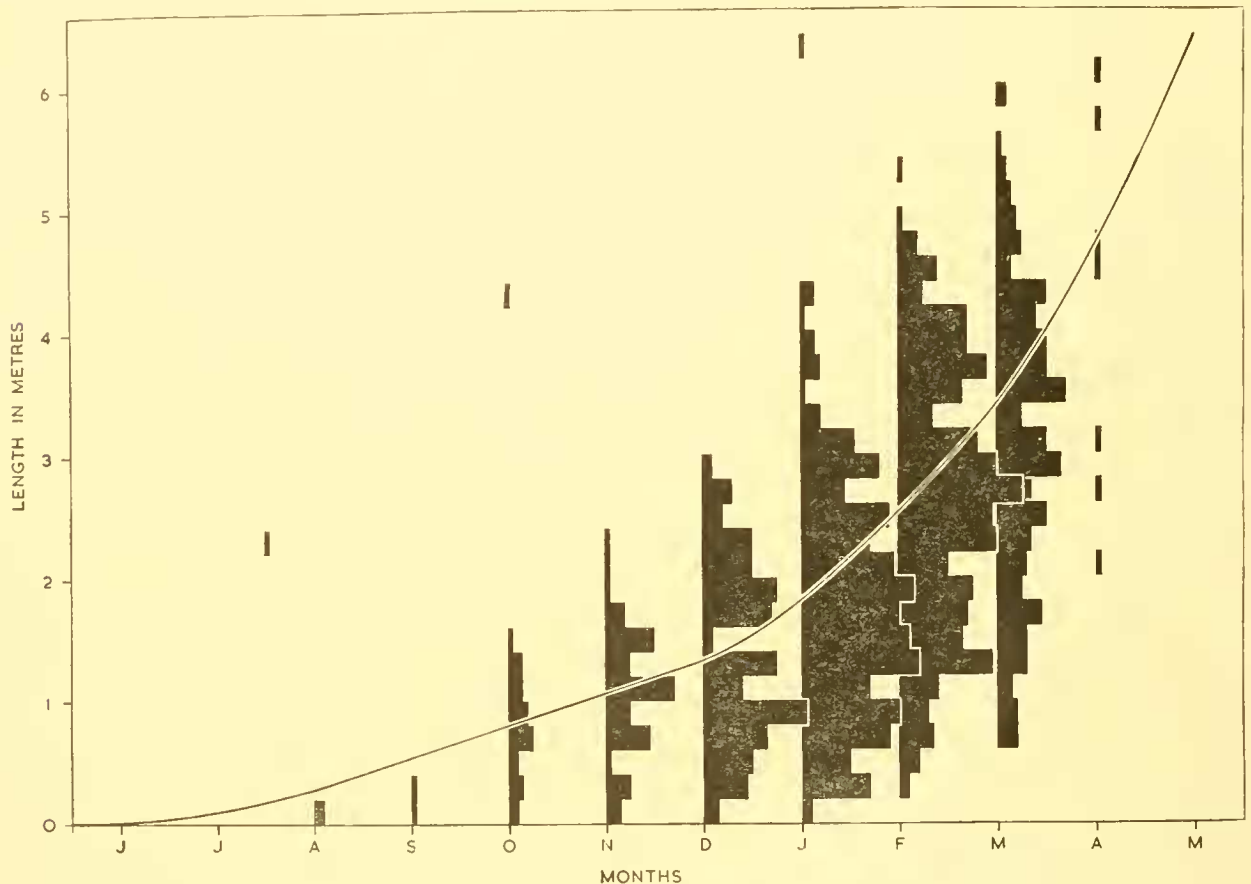
Text-fig. 9. Monthly foetal length frequencies of southern hemisphere fin whales, *Balaenoptera physalus*;
class interval 0·2 m. The estimated mean growth curve is taken from Text-fig. 8.

birth length (6·4 m., Mackintosh and Wheeler, 1929) in mid-May, giving a gestation period of just over 11 months. It is considered that this estimate is as accurate as the data permit and that it is unlikely to be more than plus or minus 15 days in error.

The reasons for concluding that the fin whale foetal length samples for March and April are biased, must now be presented.

First, it should be noted that almost all the material comes from antarctic waters. In Text-fig. 9 the monthly foetal length frequency distributions are set out in 0·2 m. groups. This figure gives a better idea of the individual variation than the same data presented in Table 2, and it will be noticed that the shape of the frequency distributions changes from month to month and that the relative numbers of larger foetuses appear to be reduced in March. The April sample is really too small to show such a tendency.

In Text-fig. 10 these monthly length frequencies have been smoothed (in groups of three), converted to percentages, and smooth curves drawn through the points thus allowing a more direct comparison to be made. It can be seen that the monthly length frequencies show a normal unskewed distribution, which is compatible with linear growth, in the early months (October and November). The later curves (December and January) are negatively skewed, suggesting an increasing growth rate. On this assumption the curves for February and March should also be negatively skewed, but the February sample shows an almost normal distribution and the March curve is positively skewed, that is to say the trend is reversed. This suggests either that the slope of the foetal growth curve has greatly decreased again (which would result in the extension of the gestation period over more than 12 months), or that some large foetuses are missing from the February sample and more are missed in March and April. The first explanation is ruled out by other considerations discussed above, and we are left with the second possibility.

Text-fig. 11 has been constructed to demonstrate the changes which may be expected in the foetal length frequency curves during the year. It has been assumed, for the purpose of discussion, that the frequency of conceptions is described by a normal curve extending over, say, 6 months (shown in the figure as an inset), that the average curve of growth in length is that given in Table 4 and Text-fig. 8, and that there is no variation in the growth rates of individual foetuses. The diagram has been constructed by plotting the average growth curve (thick line) and drawing in six similar growth curves displaced by intervals of 1 month (dotted lines). The space between these curves then extends over 6 months. This follows the practice of Mackintosh and Wheeler (1929, fig. 146). The frequency curve of foetal length has then been drawn in for each month by plotting the assumed conception frequencies against the average foetal lengths taken from the curves for each of the 6 months of conception (see inset). The frequency curves of foetal lengths constructed in this way for different sampling months demonstrate the transformation of the *shape* of the monthly length frequency curves, though not their magnitude.

The curve of conception frequencies used here is an arbitrary one and there are reasons for supposing that in the fin whale it does not show a normal distribution but is negatively skewed, i.e. the mode is earlier in time. This would have the effect of shifting the modes in the estimated foetal length frequencies for monthly samples to slightly higher values. The skewness of the curves of, for example, December, January and February would be slightly less in a more realistic model.

The shapes of these model curves are very similar to the sample length frequency curves for October, November, December, January and February (Text-fig. 10), and follow the same trend of increasing skewness and increased length range. The length frequency curve for the March sample shows a reversal of this trend and there are insufficient observations for April.

It has been suggested above that from March onwards the larger foetuses are missing from samples because females approaching full term migrate out of the Antarctic area, so as to arrive in the breeding area for parturition. Let us assume that the adult fin whale travels some 3000 nautical miles from the Antarctic feeding grounds to the subtropical breeding areas (from about 65° S. to about 15° S.); unfortunately we have no direct information on the duration of this migration. A fin whale and a blue whale each recovered some 2000 miles from the place of marking had travelled, in the Antarctic, at minimum average speeds of about 1·3 and 1·7 knots, respectively (Brown, 1957), but these speeds are undoubtedly well below the average speeds on migration. There is more useful information about the humpback whale, which is, however, a slower animal than the fin whale. Aerial observation of six migrating adults which were followed for distances of 3–20 miles showed that they travelled at speeds of 3·6–6·5 knots, averaging about 5 knots (Chittleborough, 1953). One 43 ft. male humpback marked (no. A 137) on 7 July 1953 off East Australia (*ca.* 35° 10′ S., 150° 35′ E.) was recovered

7 days later 525 miles to the north (27° S., 153° 26′ E.) having maintained an average speed of
3·6 knots in its northward migration. If the migrating near-term fin whales travel at 4–6 knots they
will take 21–31 days to cover the distance from the Antarctic to sub-tropical breeding areas. We may
therefore assume that about a month will elapse between the time of leaving the Antarctic whaling
grounds and giving birth to the calf.
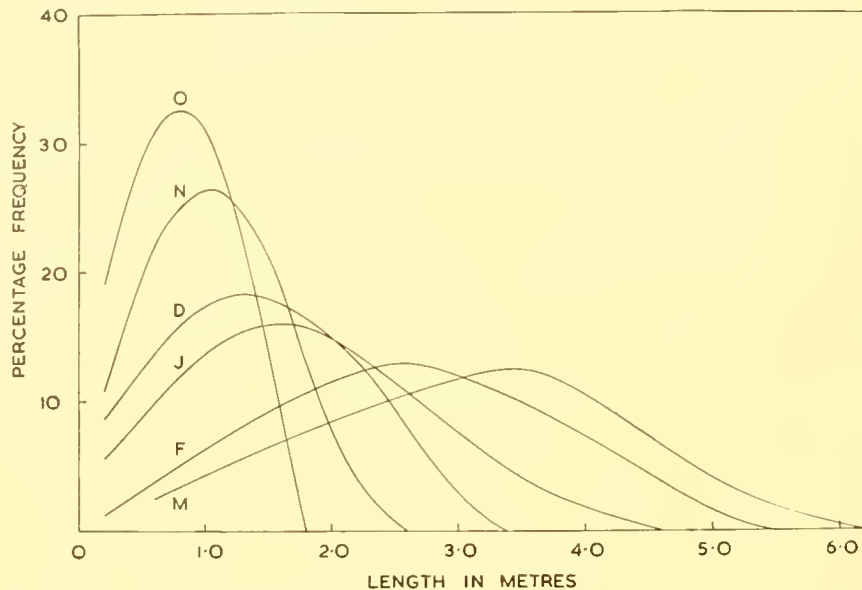
Text-fig. 10. Monthly foetal length frequencies of southern hemisphere fin whales, *Balaenoptera physalus*,
smoothed and converted into percentages.
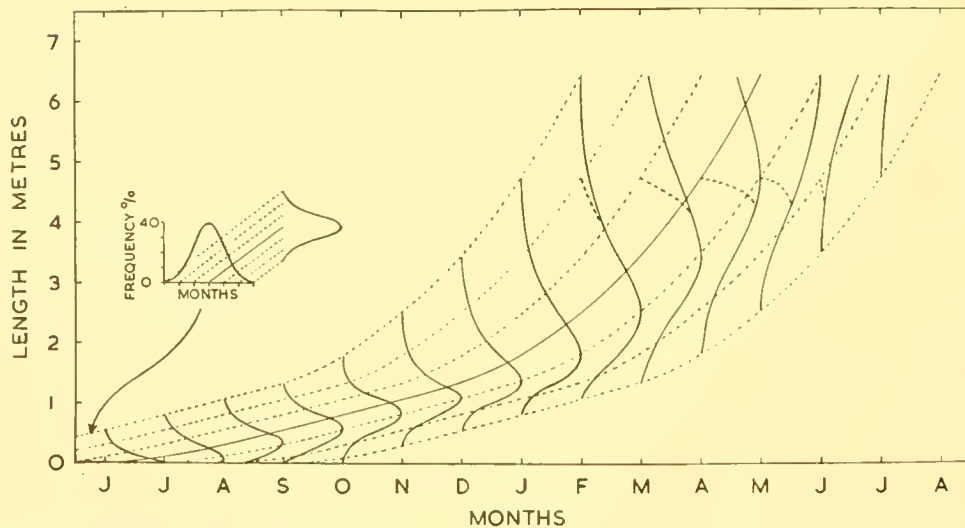
Text-fig. 11. Diagram to show expected changes in the shapes of the monthly foetal length frequencies
for the fin whale. See text for explanation.

Referring now to the average foetal growth curve for fin whales, this means that foetuses above
about 4·75 m. in length should be under-represented in the Antarctic samples. The probable effect
of this on the shape of the monthly length frequency curves is indicated in Text-fig. 11 by the broken
lines. The February sample should be only slightly affected, but from March onwards the effect on
the frequency distribution should be considerable. Thus the model frequency curve for March
becomes skewed in the reverse direction to those for December and January. This is precisely what
the actual length frequencies of the monthly samples show (Text-fig. 10).

This is undoubtedly an over-simplified picture. Conceptions probably extend over a longer period than 6 months and are not normally distributed, and there is no doubt that the individual variation in growth rates may be quite large. Kimura (1957) has shown that the differences in the body lengths of a pair of twin fin whales increases with time and suggests that at birth it will average about 2 ft. (0·62 m.). The average neonatal length of the blue whale is estimated to be 7·0 m. (Mackintosh and Wheeler, 1929), but one foetus examined at South Georgia measured 7·46 m. (Pl. XIII, fig. 2). Such variation should have no effect on the calculated average growth curves, but would explain the presence of some 7% of fin whale foetuses in the March sample which are above 5 m. in length.

Zemskiy (1950a) claimed that female embryos are larger than male embryos. He gives the mean length of sixty-six females as 247·6 cm. and of sixty-seven males as 221·1 cm. Reference to Table 4 (in the present paper) where the values of two standard errors are shown to be 12 to 19 cm. for much larger samples suggests that this supposed sex difference in growth rate is not statistically significant. Kimura (1957, p. 113) studied the lengths of pairs of twins of different sex and concluded that there is no sex difference in the rate of foetal growth.

It appears then, that foetal growth in length in the fin whale can best be described by a growth curve of the shape given in Table 4, and drawn in Text-fig. 8. It is possible that growth in the second half of pregnancy is not exponential, but if pregnancy is to occupy less that 12 months (required by the high percentage of adult females which are pregnant), then at least two more periods of differing linear growth rates are required making three in all, or the growth curve must be similar to but more complicated than an exponential curve. While this is not impossible there is no evidence for it and exponential growth appears to provide a simpler explanation. The samples taken in the Antarctic in the 5 months from October to February may be considered to be representative of the progress of foetal growth, but differential migration out of the area affects the validity of the samples from March onwards.

Four of the five foetal length records from August and September (from Saldanha Bay, South Africa) are below the calculated average lengths for these months (Text-fig. 9). In view of the small number of records, the largest of which is undoubtedly aberrant (and will be discussed later) this is statistically insignificant, but there are reasons for supposing that there is a differential migration southwards from the breeding grounds (complementary to the northward migration of near-term females from the Antarctic feeding grounds in March) so that samples from Saldanha Bay (33° S.) are likely to be biased towards small foetuses. In general, females with larger foetuses might be expected to have moved further south. It is relevant that Chittleborough (1954, 1958) found only two early embryos among several hundred recently pregnant females examined on the west coast of Australia, which suggests migration out of the area shortly after conception. Jonsgård (1951) reached similar conclusions about the minke whale on the west coast of Norway.

It is also to be expected that very early embryos (i.e. less than one month post-conception) will be absent in Antarctic samples. The effect of this on the mean foetal length would be most marked in the earlier months prior to November, for which in any case very few length records are available.

There are three foetuses in Text-fig. 9 which are conspicuously out of phase with the rest. These three foetuses are displaced by 4, 5¾ and 6 months from the average growth curve and it is thought that they represent foetuses conceived following supplementary ovulations in November to December (Laws, 1956, 1958). It is also likely that some of the smallest embryos from December onwards are the products of matings at this time. This question will be considered in more detail in a later paper, but is mentioned here for the sake of completeness and to draw attention to the wide spread of months in which conception may occur in this species.

The data for the blue whale have been examined in the same way as those for the fin whale, but it is not possible to reach such firm conclusions. Although there are more records of blue whale foetal lengths than there are for fin whales, they are spread over a shorter period (Tables 3, 5, Text-fig. 8).

It will be seen from Text-fig. 8 that a straight line could be fitted to the monthly mean values of foetal length for the blue whale which would intersect the abscissa in September, would attain 7 m. in June, and would be very much steeper than any other linear plot of foetal growth in mammalia.

Analysis of the monthly foetal length frequencies by the method used for the fin whale gives a similar picture of foetal growth to that in the fin whale, showing that growth is not linear in the second half of pregnancy. The length frequency curve for November is slightly skewed (corresponding to the December frequency distribution in the fin whale); the curves for December and January show
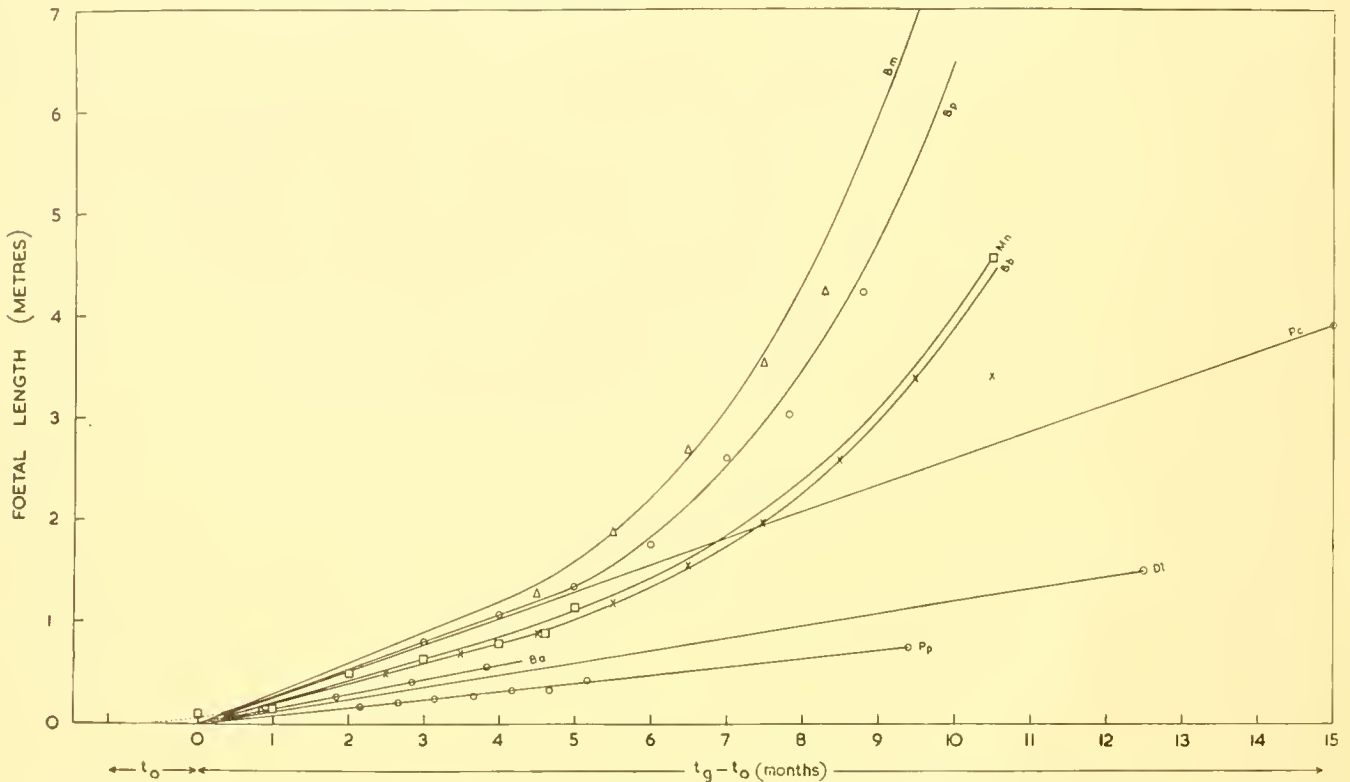
Text-fig. 12. Diagram showing estimated mean foetal growth curves of five Balaenopterids and three Odontocetes. For comparative purposes the origin of the curves is taken as t_0. (Bm = *Balaenoptera musculus*; Bp = *B. physalus*; Bb = *B. borealis*; Ba = *B. acutorostrata*; Mn = *Megaptera novaeangliae*; Pc = *Physeter catodon*; Dl = *Delphinapterus leucas*; Pp = *Phocaena phocoena*).

increased skewness, and the distributions for February and March show a reversal of this trend. The same inferences are drawn from the shapes of these monthly length-frequency distributions as for the fin whale frequency distributions, and an exponential curve has been fitted to the mean foetal lengths for November, December, January and February. This curve attains the average neonatal length (7.0 m.) in mid-April.

The slope of the linear segment of the blue whale growth curve is based on very sparse data. It has been plotted with reference to six records for October, two for September, two for August and two for July. It cuts the abscissa at the end of June and the period from conception to Lt_0 is estimated to be 30 days, slightly shorter than the similar period in the fin whale (33 days) because the slope of the linear segment of the growth curve is steeper (Table 1). This gives an estimated mean date of conception in the fourth week in May, which fits quite well with inferences made from other evidence. The estimated gestation period of the blue whale is therefore $10\frac{3}{4}$ months and although less confidence

is attached to this figure than for the fin whale estimate, it is very unlikely to be greatly in error.

The average growth curves now obtained for different species are compared in Text-fig. 12, by taking Lt_0 as the origin of the curves. For the four Balaenopterids the slopes of the linear segments of the growth curves have also been plotted against the slope of the logarithmic parts and are found to be closely correlated; the steeper the linear segment, the steeper is the logarithmic segment.

THE LENGTH/WEIGHT RELATIONSHIP

It has been shown that in the baleen whales growth in length is extremely rapid, probably following an exponential curve in the second half of pregnancy. In general, $W \propto L^3$ so the growth in weight will be even more rapid and it is therefore instructive to examine the data on the weights of whale foetuses. Zemskiy (1950b) gave records of foetal length and weight for sixty-five fin whale foetuses. Nishiwaki and Hayashi (1950) plotted weight against length for forty-three fin and blue whale foetuses, but their records were not given in tabular form and have not been used. Nishiwaki and Oye (1951) gave full information on the weights and lengths of thirty-nine fin whale, and twenty-three blue whale foetuses, and Symons (1955) gives the weight and length of one large blue whale foetus. The National Institute of Oceanography has records of foetal weights for ninety-six fin whale, seven blue whale, nine humpback whale and three sei whale foetuses making, together with published records, a total of 243 baleen whale foetuses for which length/weight records are available. All data have been converted to metric units for comparison, and the 115 previously unpublished records of foetal weight obtained by the National Institute of Oceanography are set out in Table 6. In addition Møhl-Hansen (1954) gives records of weight and length for ninety-three porpoise foetuses.

In Text-fig. 13 this material is presented graphically. The records for blue, fin and sei whales were originally plotted separately but showed no specific differences and have not therefore been distinguished. The three rather lighter than average records are fin whales. The humpback whale foetuses appear to be consistently heavier than blue, fin and sei whale foetuses of similar lengths and have therefore been given separate symbols. The plotted points for the porpoise are monthly means.

It is apparent that there is little scatter; the greater scatter at lower values is at least partly due to the limits of accuracy of the methods of weighing, how much of the umbilical cord is included, etc. For the genus *Balaenoptera* the range of variation in length between individuals of the same weight is about 20% of the mean length.

Zemskiy (1950b) examined the relationship between foetal length and weight for 100 fin whale foetuses (details of only sixty-five are given in his paper). He plotted weight against length on arithmetic scales and concluded that 'the intra-uterine development of the fin whale embryo may be divided into two stages having different features. The first period is characterized by an intensive growth in the linear dimensions of the embryo while its mass increases relatively slowly. The rapid growth in length continues until the embryo is approximately 90 cm long. The second period is characterized by an intensive growth in weight whilst the linear growth of the embryo is relatively slow' (translation). Adoption of logarithmic scales (Text-fig. 13) shows, however, that there is a *constant* relation between weight and length at least from about 30 cm onwards. The decrease in the embryonic length/weight ratio, K, used by Zemskiy is presumably only another way of expressing the known fact that $W \propto L^3$, so that weight naturally increases more rapidly than length.

The mean lengths at birth for southern blue and fin and for northern sei whales are estimated to be 7·0, 6·4 and about 4·4 m., respectively. From the regression line fitted by inspection in Text-fig. 13, these lengths correspond to birth weights of 2500 kg. (2·46 tons), 1900 kg. (1·86 tons) and 650 kg.

(0·64 tons). A regression line has also been drawn for the small series of humpback whale records which suggests a mean birth weight (at a length of 4·56 m.) of about 1300 kg (1·28 tons).

Almost all of this growth takes place in the last part of pregnancy. Mackintosh and Wheeler (1929, p. 426) pointed out that a 0·5 m. foetus 'differs very little in appearance and bodily proportions from the adult and so far as the internal structures are concerned the organs are probably all laid down by the time the foetus has reached 0·1 m. It is therefore natural to suppose that the actual linear rate

Table 6. *Length and weight data for 115 baleen whale foetuses*

Fin whale foetuses

Length (m.)	Weight (kg.)	Length (m.)	Weight (kg.)	Length (m.)	Weight (kg.)	Length (m.)	Weight (kg.)
0·26	0·32	0·9	6·4	1·42	29·0	2·76	167
0·27	0·25	0·94	5·5	1·44	26·0	2·79	200
0·31	0·4	0·95	8·5	1·45	28·5	2·83	178
0·34	0·45	0·96	9·0	1·46	29·0	2·87	190
0·35	0·85	0·96	7·5	1·48	31·0	2·9	192
0·4	0·93	1·0	11·5	1·5	29·0	2·92	191
0·47	1·2	1·0	12·0	1·5	36·5	2·95	203
0·48	1·8	1·02	11·5	1·53	33·0	2·95	203
0·48	1·76	1·04	10·0	1·59	33·5	3·03	168
0·51	1·36	1·06	11·5	1·62	43·0	3·08	228
0·52	1·4	1·08	13·0	1·78	23·0	3·13	243
0·54	1·15	1·14	14·0	1·98	64·5	3·15	234
0·59	2·04	1·15	11·4	2·03	22·5	3·22	254
0·6	1·6	1·16	14·0	2·05	79·5	3·28	279
0·6	2·3	1·16	15·5	2·12	71·0	3·35	228
0·62	3·06	1·18	17·0	2·13	91·0	3·74	433
0·62	3·05	1·24	19·0	2·15	79·5	3·86	382
0·64	2·6	1·25	19·0	2·15	79·5	4·0	471
0·66	4·3	1·27	28·0	2·24	86·5	4·05	471
0·7	3·35	1·3	19·0	2·34	97·0	4·06	509
0·75	3·6	1·3	21·5	2·43	126·0	4·23	611
0·85	5·3	1·3	27·5	2·52	147	4·3	455
0·86	5·0	1·32	19·8	2·56	137	4·48	611
0·87	5·5	1·32	27·0	2·66	153	5·4	1089

Blue whale		Humpback whale		Sei whale	
Length (m.)	Weight (kg.)	Length (m.)	Weight (kg.)	Length (m.)	Weight (kg.)
1·17	15·5	0·51	2·65	1·05	13·0
1·25	22·0	0·78	9·0	2·12	88·5
1·42	28·0	0·9	9·0	2·28	102
1·7	46·5	0·9	13·0		
2·22	100	0·95	14·5		
3·14	272	1·0	17·6		
3·5	365	1·05	21·8		
		1·17	31·0		
		1·24	23·5		

of growth is extremely slow while the foetus grows from zero to about 0·1 m. compared with its subsequent growth up to the end of gestation, for from between 0·1 and 0·5 m. up to birth at 6–7 m. development consists mainly in increase in size.' Comparison of Pl. XIII, figs. 1 and 2, illustrates this point. The 18·5 cm. foetus shown in fig. 1 is already typically cetacean in appearance (2 months after conception) and even at this age does not differ very markedly in bodily proportions from the 7·46 m. foetus illustrated in fig. 2.

Zemskiy (1950*b*, figs. 2, 3) demonstrated this by means of detailed measurements of sixty-six fin whale embryos between 49·5 and 569 cm. in length. He took five series of measurements (snout-umbilicus; snout-anus; head length; pectoral girth; anal girth) and showed that the ratio of these measurements to body length (expressed as percentages) remained more or less constant within this range of foetal lengths. The smaller series of foetal measurements given by Mackintosh and Wheeler (1929, pp. 324–29) are in very close agreement. These authors also give the results of similar measurements on over 600 post-natal fin whales. Their mean percentage values for these three linear proportions in adults are very close to the mean values for foetuses and well within the foetal ranges.

Zemskiy states that the throat grooves (a special feature of the rorquals) first become apparent at a length of 1·0 m., and become distinct and similar in appearance to those of the adult at a length of 1·5 m. The baleen is first discernible externally in embryos of about 3·0–4·0 m. (Mackintosh and Wheeler, 1929, fig. 96; Zemskiy, 1950).
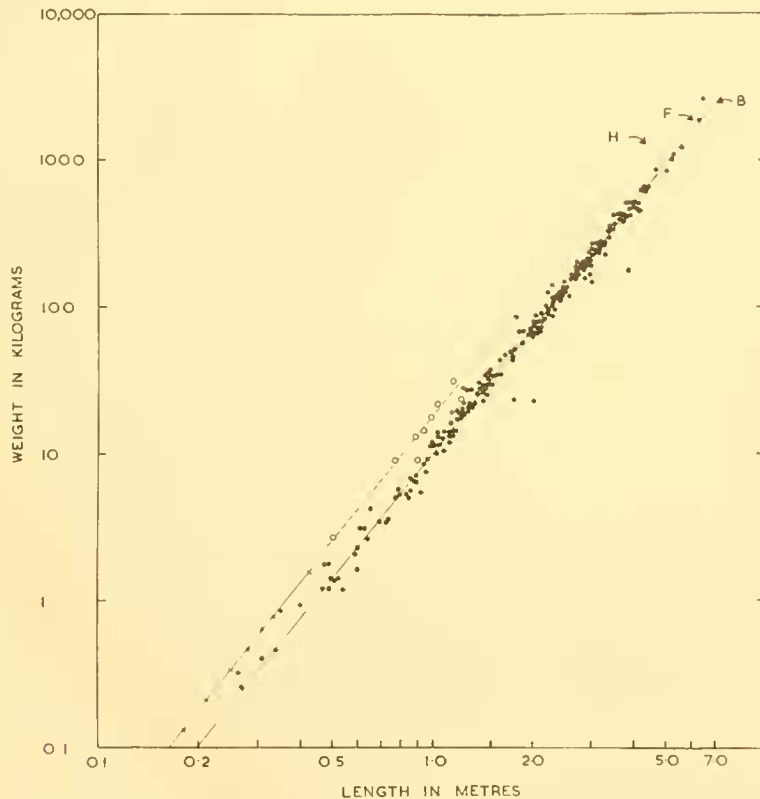
Text-fig. 13. Plot of foetal weight against length for 234 blue, fin and sei whales (black circles), nine humpback whales (white circles), and ninety-three porpoises (crosses=monthly mean values). Regression lines have been fitted by eye and the neonatal values for blue, fin and humpback whales are indicated.

In the last 5 months of pregnancy the blue whale foetus grows in length from 1·3 to 7·0 m., corresponding to an increase in weight of 2480 kg. (from 20 to 2500 kg.) or 2·44 tons. In the last *two* months of pregnancy the average gain in weight is over 2 tons (420–2500 kg). The growth rate of the fin whale is of the same order of magnitude. In some individual blue whales the growth rate is probably even greater; the largest blue whale foetus (Pl. XIII, fig. 2) measured 7·46 m. and must have weighed about 2800 kg. (2·75 tons).

Expressed in this way the foetal growth rate of the baleen whales is seen to be phenomenally rapid, and without parallel.

CONCLUSIONS

Previous papers dealing with foetal growth of whales and with the breeding season and the gestation period have attacked the problem by plotting the mean monthly foetal lengths and then drawing in a curve by eye. The method developed by Huggett and Widdas (1951) for dealing with foetal length and weight data appears to hold good for the three species of toothed whales considered in this paper and to a limited extent for the five Balaenopterid species which have been studied. In particular this method provides for an objective estimate of the length of the initial period of very slow growth before the placental circulation is fully established. This is impossible by means of freehand extrapolation.

Huggett and Widdas (1951, p. 314) remark that in 'mammals in the intermediate range of [their] fig. 8, the period of linear growth is determined by the size of the foetus at birth. Thus, as the birth weight of the young is increased the mammal does not grow its young quicker, along a steeper slope, but must grow its foetus for a longer time. This will offer an explanation of Rubner's finding in 1908 that in all species except man the birth weight is proportional to the gestation time.'

It will be apparent that this is not true of the marine mammals which have been studied. In most species of seals the period of foetal growth is of more or less equal duration, but the birth weight of the largest species is ten times that of the smallest species. Increased size at birth is attained by increasing the growth rate, rather than by extending the gestation period. In the toothed whales which have been studied, increased size at birth appears to be attained both by increasing the rate of growth and by extending the period of gestation, as in the sperm whale.

The growth velocities of the species of toothed whales studied fall within the ranges $a \simeq 0.05$ and $a \simeq 0.02$ (for weight) as do all the species of mammals considered by Huggett and Widdas (1951, fig. 8), with the conspicuous exception of the fin and blue whales. In the Balaenopterids, the evidence discussed in this paper shows that for the first part of gestation the growth velocity is within this range, but the growth rate (for L or $W^{\frac{1}{3}}$) probably increases exponentially after the fifth month of pregnancy. In all Balaenopterid species the gestation period is 12 months or less and the very large neonatal sizes are attained by this phenomenal burst of growth in the second half of pregnancy, not as in the sperm whale by extending the gestation period. In fact, it appears that in the genus *Balaenoptera* there is a tendency to shorten the gestation period in association with this increased growth.

Huggett and Widdas (1951) were unable from their data to suggest any biochemical or physiological reason why growth should conform to a cube root law, and it is even more difficult to see why baleen whale foetuses should follow an exponential cube root law.

For some fundamental reason the gestation period of the rorquals does not exceed 12 months whereas in the sperm whale it is possible for gestation to occupy 16 months. One of the most conspicuous differences in the behaviour of baleen whales as compared with the toothed whales is the very discontinuous feeding cycle of the former. Almost all baleen whales must enter polar waters to feed at a time when their planktonic food is available in suitable quantity; when not feeding it is probable that they must seek warmer waters where energy loss due to heat radiation is less. The period when food is available in amounts large enough to make its collection economical for the whales is limited in the Southern Ocean to a period of 3 or 4 months (Marr, 1956) although some animals move south before this period and others stay in polar waters later (see Mackintosh and Brown, 1956, fig. 2). During the feeding period the baleen whales lay down thick reserves of blubber (Ash, 1956) on which they draw for the remainder of the year.

Most Balaenopterid species have a 2-year sexual cycle, comprising a gestation period of less than a year, lactation occupying about 6 months and the remaining 6 or 7 months in anoestrus. Conception

and calving take place in winter in low latitudes and the annual feeding migrations occur in mid-pregnancy and at the end of lactation or beginning of the anoestrus period.

If the initial linear phase of growth were to persist it can be shown by extrapolation that the gestation periods would have to be approximately doubled in order to attain the present neonatal sizes. One effect of this would be to reduce the reproductive rate very greatly. Conversely, if gestation were limited to 12 months and the present linear growth persisted throughout, the birth sizes would be only half the present sizes. If the gestation periods, or the neonatal sizes, were intermediate between these extremes, then it seems probable that the reproductive cycle would be out of step with the feeding cycle. For instance, with a gestation period of 18 months, other things being equal, parturition would occur in the Antarctic and the chances of survival of the calf might well be affected.

With regard to feeding habits, the difference in the nature of the food is also perhaps significant and it is interesting that in the blue, fin, sei and humpback whales the beginning of the great burst of growth is associated with the arrival of these species on the polar feeding grounds. Little or nothing is known of foetal growth in a temperate zone species like *B. brydei*, which is presumably subject to rather different feeding conditions.

The evidence for a period of exponential growth is by no means conclusive and it may be that growth could be described by a series of successive growth cycles. It should be noted that if exponential growth is adopted as a means of increasing neonatal size, the duration of the growth period must be kept relatively short, because a small increase in the length of the growth period will entail a disproportionately great increase in the neonatal size, which is of course limited by the size of the mother. Similarly, an increase in the slope of the curve of exponential growth may cause a very large increase in the final size. In the blue whale, for instance, it is estimated that an increase of half a month in the length of the gestation period to bring it into line with that of the fin whale would, if growth is exponential, result in a neonatal length of 8·4 m., corresponding to a weight of about 4000 kg. or 3·93 tons; that is an increase of 60% in the birth weight for a gestation period only half a month longer. In the larger baleen whales a shortening of the gestation period is seen to be essential if the slope of the growth curve is further increased and on the evidence at present available this appears to be the general trend in the large Balaenopterids.

SUMMARY

1. The literature on foetal growth in whales is reviewed.

2. It is shown that foetal growth in three species of toothed whales can be described by a linear plot of length. The method of Huggett and Widdas (1951) is used to estimate the duration of the non-linear early part of pregnancy and so to estimate mean conception dates and gestation periods.

3. In the toothed whales studied larger neonatal sizes are attained by increased rates of growth and by extension of the gestation period.

4. In the baleen whales the first half of pregnancy follows this law, but thereafter growth can best be described by a logarithmic plot of length or of the cube root of weight. So far as is known this is unique among mammals.

5. Original foetal length data for 956 southern fin whales and 1022 blue whales are presented, examined and discussed. Mean foetal growth curves (length) are given for southern hemisphere fin and blue whales.

6. The average duration of gestation is estimated to be $11\frac{1}{4}$ months (early June to mid-May) in the southern fin whale; $10\frac{3}{4}$ months (end of May to mid-April) in the southern blue whale.

7. The length/weight relationship of foetal baleen whales is examined, the data comprising 243 records of foetal length and weight. The mean lengths at birth for southern hemisphere blue,

fin and humpback whales and for the northern sei whale are estimated to be 7·0, 6·4, 4·56 and about 4·4 m. The corresponding birth weights are 2500 kg. (2·46 tons), 1900 kg. (1·86 tons), 1300 kg. (1·28 tons) and 650 kg. (0·64 tons).

8. Most of this growth takes place in the last 2 months of pregnancy. In the blue whale the average gain in foetal weight during this period is over two tons.

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PLATE XIII

Fig. 1. An 18·5 cm. fin whale foetus (male).
Fig. 2. A 7·46 m. blue whale foetus (male), estimated weight 2·75 tons.
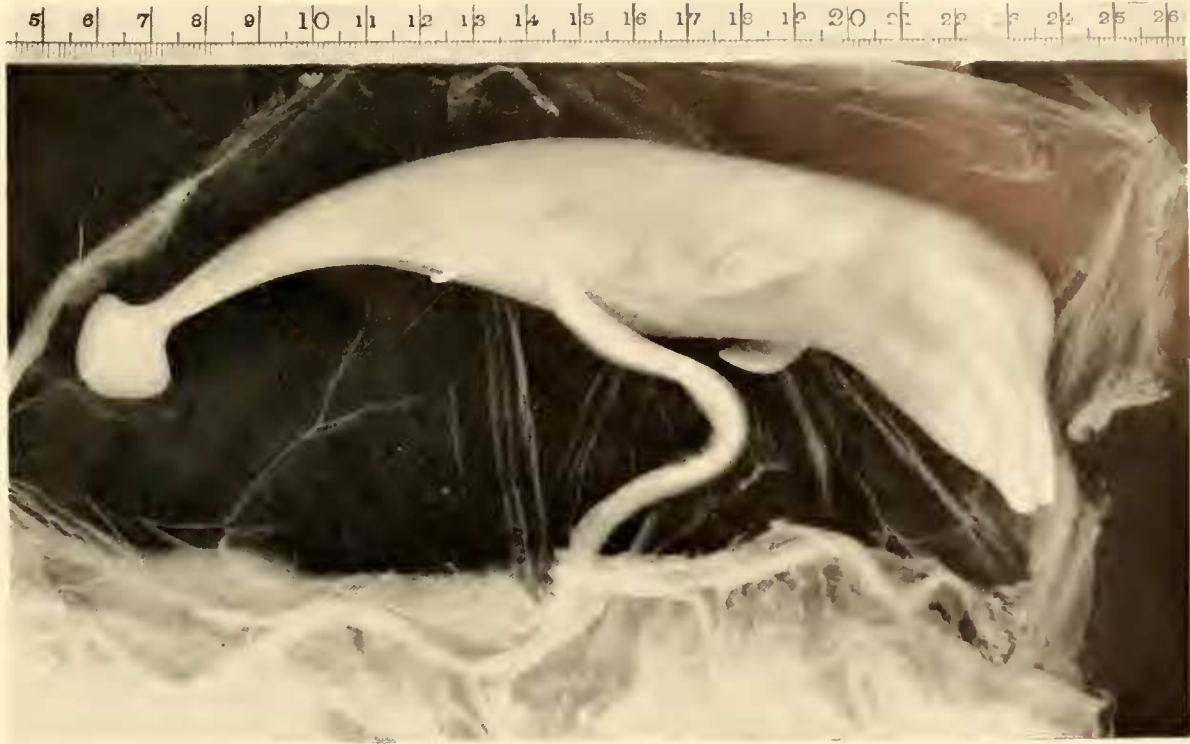
(*photo: N. A. Mackintosh*)

Fig. 1

Fig. 2